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THE SYSTEMATICS AND BREEDING SYSTEM OF GELSEMIUM (LOGANIACEAE)

ROBERT ORNDUFF

THE LOGANIACEOUS GENUS *Gelsemium* exhibits a pattern of distribution that has interested plant geographers and systematists for over a century (Gray, 1846, 1859; Hara, 1952, 1956; Miranda & Sharp, 1950; Li, 1952). The genus is represented by one species in southeastern Asia, a second species in the southeastern United States, and a third species in the southeastern United States and the highlands of southern Mexico and Guatemala. This distribution pattern is similar to that which occurs in a number of other taxa of flowering plants. Although this disjunction dates back to the close of the Tertiary, *Gelsemium* has continued to maintain a relatively high degree of morphological and genetic homogeneity. The purpose of this paper is to present a general systematic account of *Gelsemium* and to discuss the breeding system which is associated with heterostyly in the genus.

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RELATIONSHIPS

The relationships of *Gelsemium* ($n = 8$, see below) to other genera of Loganiaceae are not at all clear. In their description of the Asian species in 1849, Gardner and Champion suggested an affinity with the African *Usteria* ($n = 11$; Miège, 1960) and the South American *Antonia* based on similarities of capsule structure. Bentham (1876) placed *Gelsemium*,

the African-South American *Mostuea* ($n = 10$; Gadella, 1962, 1963), and the Central American *Plocosperma* together in the tribe *Gelsemieae*. The occurrence of distyly (Leeuwenberg, 1961) and indole alkaloids (Leenhouts, 1962) in both *Gelsemium* and *Mostuea* supports the morphological evidence indicating that these genera are allied, but the cytological data do not conclusively support this affinity. Moore (1947) indicated that *Gelsemium* has an isolated position in Loganiaceae and might have closest affinities with Apocynaceae, although he favored retention of the genus in the first family.

Despite the number of generic names that have been applied in *Gelsemium*, the only attempt to discriminate between New World and Asian species at the generic level was that of Gardner and Champion, who distinguished the Asian *Medicia* from *Gelsemium* because the former has "imbricated, not quincuncial, aestivation of the corolla, inflated capsule, and numerous peltate, compressed seeds surrounded on all sides by a broad inciso-dentate membranous wing." The differences in aestivation are slight and the seeds of *G. sempervirens* are asymmetrically winged, thus leaving the capsule character as the sole one which might be used for a generic distinction. I am, therefore, inclined to follow the tradition of other workers in recognizing only a single genus. Nevertheless, the Asian species is considerably more different from the two American species than these are from each other.

Chromosome numbers of $2n = 16$ have been obtained for the three species of *Gelsemium* (TABLE 1; Moore, 1947; Gadella, 1963). All chromosome counts reported in this paper were made on mitotic tissue of shoot apices with the exception of a single meiotic count obtained from microsporogenous tissue in *G. sempervirens*. Recently Duncan and DeJong (1964) have reported $2n = 8$ for *G. rankinii* based on sectioned material in which counts of $2n = 9$, 10, and 16 were also noted. Because of the variation in the number of chromosomes they observed, the difficulties in interpreting sectioned material (see, for example, Epling, Lewis, & Raven, 1962), and the consistent chromosome number of $2n = 16$ that I have obtained for this species from several localities, Duncan and DeJong's report and the evolutionary conclusions based upon it are open to question.

Attempts to produce artificial hybrids from legitimate crosses between *Gelsemium sempervirens* and *G. rankinii* resulted in low seed production (TABLE 2). All hybrid seed was planted, but the germination percentage was also very low. A total of eleven hybrid plants has been obtained, but these are considerably less vigorous than seedlings of the parental species. Most of the hybrids died a few months after germination and the remainder have been slow to produce flowers. The only hybrid which has flowered is one individual obtained from a cross between *Breedlove 9005* (*G. sempervirens*, Chiapas, Mexico) and *Godfrey 62671* (*G. rankinii*, Liberty County, Florida). This plant produced a single flower with pollen having an 81% viability, based on the stainability of a sample of 200 pollen grains mounted in aniline blue-lactophenol. However, when it was

backcrossed to both parents only five seeds matured in the capsule. In pedicel, sepal, and capsule characters the hybrid resembled *G. rankinii*, but the winged seeds were similar to those of *G. sempervirens*. Thus, these two species are separated by barriers to crossing, by low germinability of hybrid seed, and by reduced viability and fecundity of the hybrids.

Some plants of the Guatemalan and Mexican populations of *G. sempervirens* are indistinguishable from those in the United States, but others have leathery, dark green, glossy, involuted leaves, as well as a tendency for higher numbers of flowers in each inflorescence. In addition, these Meso-American plants apparently have unscented flowers, whereas flowers of this species in the United States have a very strong fragrance.

TABLE 1. **Chromosome numbers of Gelsemium**

COLLECTION DATA	LOCALITY	CHROMOSOME NUMBER
G. SEMPERVIRENS:		
L. E. Anderson, s.n.	Durham County, North Carolina	$n = 8$
Ornduff 6376	Hoke County, North Carolina	$2n = 16$
Ornduff 6707	Richland County, South Carolina	$2n = 16$
Breedlove 9005	Pueblo Nuevo Solistahuacán, Chiapas, Mexico	$2n = 16$
G. RANKINII:		
G. B. Newcomb, in 1965	Tammany Parish, Louisiana	$2n = 16$
R. Godfrey 62667	Liberty County, Florida	$2n = 16$
R. Godfrey 62671	Liberty County, Florida	$2n = 16$
R. Godfrey 62673	Franklin County, Florida	$2n = 16$
G. ELEGANS:		
S. C. K. Chan, s.n.	Hong Kong	$2n = 16$

A few hybrids have been obtained from a cross between some plants of *G. sempervirens* from Chiapas, Mexico, and others from Durham County, North Carolina. These parental populations are from the extreme ends of the range of this species. The pollen viability of the two hybrid plants that have flowered at the time of writing is 100% (based on a sample of 100 grains mounted in aniline blue-lactophenol). This suggests that the somewhat divergent morphological and biochemical characters (i.e., lack of flower odor) of the geographically disjunct parental populations are not associated with sufficient genetic discontinuities to result in lowered pollen viability of hybrids obtained from a wide geographical cross.

TOXIC PROPERTIES

The herbage of *Gelsemium* contains several toxic alkaloids (Debay, 1950; Martínez, 1959; Kingsbury, 1964). *Gelsemium sempervirens* causes death and abortion in livestock which feed upon its leaves (Hardin, 1961; Kingsbury, 1964). Ingestion of nectar and honey produced from *Gelse-*

mium flowers reportedly has caused death in humans and bees in the southeastern United States (Kingsbury, 1964). Information concerning *G. elegans* indicates that this species has been used in China, Viet Nam, and Borneo as a suicidal poison which is either ingested or smoked. A note with *Khant 15216* (K) states that this species is used as a fish poison in Burma. The label of *Dickason 9789* (GH) reports that the flowers of *G. elegans* are "poisonous to smell! Kills butterflies on the flowers." It has been stated (*Gibbs* in 1910, BM) that in Borneo this species is "much used for feeding pigs . . . but is very poisonous to man."

Despite its toxic properties, *Gelsemium sempervirens* is frequently grown in the gardens of the southeastern United States and of California, where it is prized for its heavily fragrant yellow flowers. It has been cultivated in Europe since the mid-17th century.

TAXONOMY

Gelsemium Jussieu, Gen. Pl. 150. 1789.

Jeffersonia Brick., Med. Rep. N.Y. **1**: 555. 1800.
Medicia Gardn. & Champ., Hook. Jour. Bot. **1**: 324. 1849.
Leptopteris Blume, Mus. Bot. Lugd. Bat. **1**: 240. 1850.

Type species: *G. sempervirens* (L.) Jaume Saint-Hilaire.

Twining woody vines; leaves opposite, simple, entire, petiolate; stipules represented by stipular lines; flowers pentamerous, distylous or homostylous, 1 to many, in axillary or terminal inflorescences; corollas funnelform, the lobes imbricated in bud, bright yellow or orange-yellow; stamens five, epipetalous; style quadrifid at apex; ovary two-locular; fruit a capsule; seeds flattened, usually winged; $n = 8$.

KEY TO THE SPECIES

1. Flowers 2.0–3.5 cm. long, borne in inflorescences of 1–8 flowers; capsules not inflated; seeds wingless or with a strongly asymmetrical entire wing. . . . . 2.
   2. Sepals obtuse, deciduous in fruit; upper half of pedicels bracteolate; capsules terminated by a very short inconspicuous beak; seeds with a strongly asymmetrical, essentially unilateral wing; flowers usually strongly scented. . . . . 1. *G. sempervirens*.
   2. Sepals acuminate, persistent in fruit; upper half of pedicels ebracteolate; capsules terminated by a conspicuous beak; seeds lacking wings; flowers usually odorless. . . . . 2. *G. rankinii*.
1. Flowers 1.2–1.7 cm. long, borne in inflorescences of numerous flowers; capsules inflated; seeds surrounded by an inciso-dentate wing. . . . 3. *G. elegans*.

1. **Gelsemium sempervirens** (L.) Jaume Saint-Hilaire, Expos. Fam. Nat. **1**: 338. 1805 (Feb.-Apr.).

Bignonia sempervirens L. Sp. Pl. **2**: 623. 1753.
Gelsemium nitidum Michx. Fl. Bor. Am. **1**: 120. 1803. Holotype: P (photograph! GH).

Gelsemium lucidum Poir. Encycl. Méth. Bot. Suppl. 2: 714. "1811" (3 July 1812). Holotype: P?

Lisianthus sempervirens Mill. ex Steud. Nomencl. (ed. 1) 358. 1821.

Leaves lanceolate to narrowly ovate, the blades 3–7 cm. long, more or less evergreen, the petioles 0.3–0.5 cm. long; flowers 1–8, corolla 2.5–3.5 cm. long, including the lobes 0.8–1.2 cm. long, bright- to orange-yellow, darker in throat, strongly fragrant (rarely odorless); sepals elliptic, obtuse, 3–5 mm. long, mostly deciduous in fruit; pedicels 0.2–1.2 cm. long, usually densely bracteolate throughout; capsules broadly oblong, 1.5–2.5 cm. long, terminated by a very short beak 0.1–0.2 cm. long representing the base of a deciduous style, woody, hard, tardily dehiscent; seeds brownish, 1.2–1.5 cm. long, including an asymmetrical wing to 1.0 cm. long; $n = 8$. Flowers (January) February–April (May) and occasionally again in late summer or early autumn. FIG. 1a–d.

DISTRIBUTION. Sea level to 6000 feet (in Mexico and Guatemala). Climbing on fences, low bushes, and trees, or prostrate on ground. Pine or deciduous woodlands in damp to very dry soil, southeastern Virginia to Florida to eastern Texas; mountains of Mexico and Guatemala (FIG. 3).

Representative specimens: **United States.** ARKANSAS. Bradley Co.: Warren, *Demaree 14364* (GH, NY), *Demaree 14387* (NY). Calhoun Co.: Hampton, *Demaree 14407* (NY). Cleveland Co.: Rye, *Demaree 13568* (NY). Faulkner Co.: Near Republican, *Demaree* in May 1925 (A); near Holland, *Palmer 26534* (A). Hot Springs Co.: Malvern, *Demaree 14493* (GH, NY). Miller Co.: 14 miles east of Texarkana, *Harrison* in 1946 (GH). Monroe Co.: Little Rock, *Manning 85* (GH). Pulaski Co.: Near Ledwidge, *Demaree 8890* (A, NY). FLORIDA. Desoto Co.: 6 miles north of Arcadia, *Ward & Ward 2825* (FLA). Hernando Co.: Brooksville, *Jones* in 1919 (A); Brooksville, *Jones* in 1920 (NY, US). Highland Co.: Sebring, *Hunnewell 9029* (GH). Hillsborough Co.: No definite locality, *Fredholm 6245* (GH). Manatee Co.: Manatee, *Simpson* in 1898 (US); vicinity of Manatee, *Simpson 5* (US). Orange Co.: No definite locality, *Smith* in 1886 (MICH). Pasco Co.: Ehren, *Riegler* in 1961 (FLA); no definite locality, *Barnhart 2518* (NY). Pinellas Co.: No definite locality, *Frank* in 1900 (NY). Polk Co.: Near Lake Marion, *McFarlin 4505* (MICH); Bartow, *McFarlin 6637* (MICH). Sarasota Co.: Sarasota, *Perkins* in 1943 (GH). TENNESSEE. Hamilton Co.: 3 miles from Sole Creek, *Prather 284* (NY). No definite locality, *Leonard 4133* (US). TEXAS. Angelina Co.: 4 miles northwest of Jasper, *Cory 52589* (GH, NY); 7 miles southwest of Lufkin, *Cory 49746* (GH, NY, UC, US). Hardin Co.: Southwest of Hooks Switch, *Cory 52693* (NY); Saratoga, *Bailey 941* (US); north of Sour Lake, *Lundell & Lundell 10882* (UC, US). Harris Co.: Houston, *Fisher 14* (US), *Hall 512* (GH, NY, US). Montgomery Co.: Near Conroe, *Palmer 33330* (A). Nacogdoches Co.: 5 miles south of Nacogdoches, *Lundell & Lundell 9761* (MICH, US). Newton Co.: 22 miles south of Newton, *Cory 10914* (GH). Polk Co.: Indian Reservation, *Girvin* on Jan. 31, 1940 (GH, UC); Livingston, *Palmer 5192* (A, MICH, US), *Palmer 6795* (A, US); near Rye, *Traverse 300* (GH). San Jacinto Co.: Without definite locality, *Tharp* in 1935 (MICH, US). Shelby Co.: Five miles north of Center, *Rowell, York & Tharp 47243* (DUKE, GH, NY, UC, US). Tyler Co.: Hyatt Bog, 16 miles south of Woodville, *Cory 52710* (GH, NY). Walker Co.: Near Huntsville, *Tharp* in 1946 (DUKE, NY, UC). VIRGINIA. Greens-

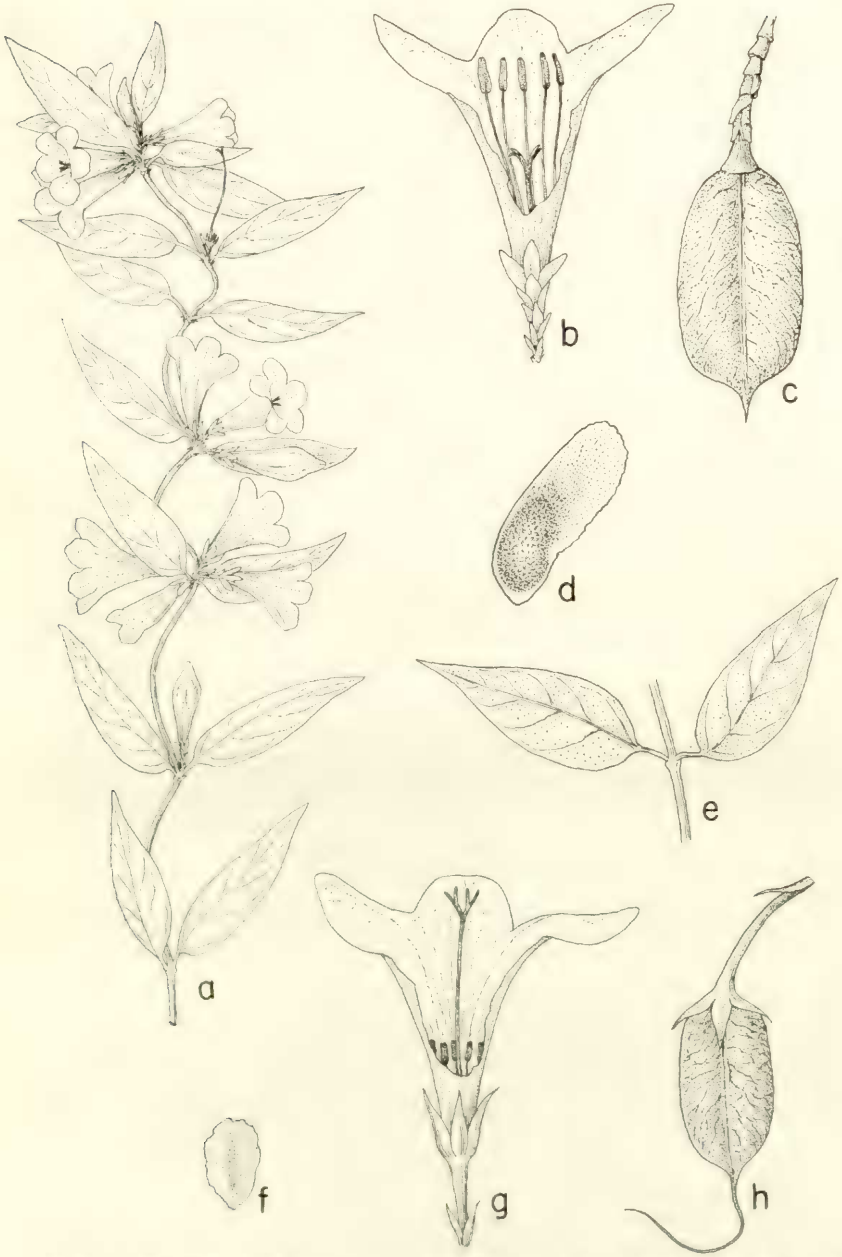

FIG. 1. Characters of *Gelsemium sempervirens* and *G. rankinii*. a–d, *G. sempervirens*. a, habit of flowering stem, × 0.5; b, partly dissected short-styled flower. × 1.5; c, capsule prior to dehiscence, × 2; d, seed, × 3; e–h, *G. rankinii*. e, portion of stem showing rounded leaf-bases often found in the species, × 0.5; f, seed, × 3; g, partly dissected long-styled flower, × 1.5; h, capsule prior to dehiscence, × 2.

ville Co.: Skipper's, *Fernald & Long 7143* (GH). Isle of Wight Co.: South of Lee's Mill, *Fernald, Long & Abbe 14224* (GH); south of Zuni, *Fernald & Mooré 15146* (GH, NY, US). James City Co.: Hampton, *Miller* in 1903 (US); 5 miles west of Toano, *Baldwin 101* (GH); southwest of Williamsburg, *Grimes 2565* (NY); near Williamsburg, *Maxon 10614* (BM, MICH, US). Nansemond Co.: Near Crismond, *Fernald & Long 7142* (GH, US); edge of Dismal Swamp, *Gleason 8617* (NY). Northampton Co.: Savage Neck, *Fernald, Long & Fogg 5411* (GH). Princess Anne Co.: Cape Henry, *Egler 40–180* (NY); Dismal Swamp, *Coville & Kearney 101* (US), *Morong* in 1877 (NY), *Seaman* s.n. (NY, US), *Ward* in 1877 (US); vicinity of Norfolk, *Jensen* in 1907 (A, US); Virginia Beach, *Bartram* in 1908 (GH), *Hollick & Britton* in 1890 (NY, US), *Britton* in 1892 (NY); south of Virginia Beach, *Britton & Small* in 1893 (NY); near Virginia Beach, *Coville & Kearney 17* (US); Virginia Beach, *Fernald & Griscom 2876* (GH), *Stevens* in 1894 (US); without definite locality, *Kearney 1168* (A, US). Southampton Co.: Meherrin River, *Fernald & Long 7141* (GH, NY). Surry Co.: West of Bacon's Castle, *Fernald & Long 7950* (GH). Sussex Co.: Near Moore's Mill, *Fernald & Long 7140* (BM, GH); Spring Grove, *Eaton* in 1938 (GH); northeast of Sussex Courthouse, *Fernald, Long & Abbe 14223* (GH, NY, US). **Guatemala.** ALTA VERAPAZ: Coban, *von Türckheim 881* (GH, K, NY, US), *von Türckheim 1648* (GH, NY, US). ZACAPA: Slopes of Monte Virgen, *Steyermark 42625* (US); between Loma El Picacho and Cerro de Monos, *Steyermark 42773* (A, NY, US). **Mexico.** CHIAPAS: Lagunas de Monte Bello, *Rzedowski 697* (MICH); Pueblo Nuevo Solistahuacán, *Breedlove 9005* (DS, UC). HIDALGO: About 4 miles from Zacualtipán, *Moore 2337* (GH, UC). OAXACA: Talea, *Galeotti 1605* (US). PUEBLA: Zacatlán, *Salazar* on Apr. 3, 1913 (US). VERA CRUZ: Jalapa, *Halsted* s.n. (NY), *Pringle 7766* (GH, MICH, UC), *Smith 1876* (NY, UC); Orizaba, *Botteri 934*, s.d. (BM, K).

In his protologue dealing with this species, Linnaeus (1753) does not cite any specimens except one in Van Royen's herbarium; all other citations are of illustrations and written descriptions. Van Royen's specimen at Leiden lacks flowers and fruits and is, therefore, not unequivocally referable to *G. sempervirens* rather than to *G. rankinii*. Since Linnaeus described fruits, he obviously had more in mind than Van Royen's material alone.

It is quite clear that the Linnaean protologue describes what we now call *Gelsemium sempervirens*. Furthermore, there is no evidence that *G. rankinii* had been collected before the early 19th century, whereas *G. sempervirens* was well known as a cultivated ornamental in Europe as early as the mid-17th century. Although the Van Royen specimen most likely is *G. sempervirens*, I am reluctant to designate it as a lectotype since vegetatively *G. sempervirens* and *G. rankinii* are not easily distinguishable (see Duncan & DeJong, 1964).

The Catesby illustration (1731) is too generalized to be referable to one of these species, but his written description (mentioning fragrance, winged seeds, and geographical distribution) clearly indicates that he was illustrating and describing *G. sempervirens*. So far as I can determine no herbarium material of this species known to have been seen by Catesby exists (see Dandy, 1958), and Catesby himself indicates that he drew largely from nature. Ray's *Historia Plantarum* has a description also

mentioning odor and winged seeds, but there is no indication that a specimen (or illustration) exists. The Plukenet drawing (1696) is very crude, although the winged seeds indicate that he was illustrating *G. sempervirens*. I am designating the illustration by Plukenet as the lectotype of *G. sempervirens* since it is supported by a specimen in the Sloane Herbarium (H.S. 90: 55) at the British Museum which was probably collected by Banister.

I consider *G. nitidum* to be a synonym of *G. sempervirens*. In the Michaux Herbarium at the Muséum National d'Histoire Naturelle in Paris there are three sheets of *Gelsemium* that bear specimens which were presumably collected by Michaux. Two of these sheets bear specimens of *G. rankinii* and the third has *G. sempervirens*. The only sheet annotated as *G. nitidum* is one of those with specimens of *G. rankinii*. Although Michaux had a mixed collection available when he described *G. nitidum*, his characterization of the flower odor indicates that he had *G. sempervirens* in mind. For this reason I do not believe that *G. nitidum* can be considered as the earliest correct name for *G. rankinii* and would suggest that there are good grounds for considering *G. nitidum* as a *nomen confusum*.

2. **Gelsemium rankinii** Small, Addisonia 13: 37. 1928. "Swamps of the Waccamaw River near Hallsboro, North Carolina, collected by *H. A. Rankin*, April 17, 1928." Holotype: NY!

Gelsemium sempervirens (var.) *inodorum* Nutt. Gen. N. Am. Pl. 171. 1818. Holotype: BM! Collected near Savannah, Georgia.

Leaves lanceolate to narrowly ovate, the blades 3.0–7.5 cm. long, more or less evergreen, the petioles 0.3–0.6 cm. long; flowers 1–8; corolla 2.0–3.5 cm. long, the lobes 0.8–1.5 cm. long, bright- to orange-yellow, darker in throat, usually odorless; sepals lanceolate, acuminate, 3–6 mm. long, persistent in fruit; pedicels 0.2–1.0 cm. long, ebracteolate on upper half; capsules oblong, 1.0–1.6 cm. long, terminated by a persistent stylar beak 0.2 cm. long, woody, hard, tardily dehiscent; seeds brownish, 3–4 mm. long, wingless; $n = 8$. Flowering (February) March to April and rarely again in early autumn. FIG. 1e–h.

DISTRIBUTION. At low elevations, climbing on fences, low bushes, and trees, or prostrate on ground. Wet woodlands or swamps of the coastal plains of North Carolina (rare), southern Georgia, northern Florida, southern Mississippi, and southeastern Louisiana (FIG. 3).

Specimens examined: ALABAMA. Escambia Co.: Atmore, *Blanton 206a* (MICH). Mobile Co.: Citronelle, *Milligan* in 1903 (US). FLORIDA. Bay Co.: Between Southport and Westbay, *Hume* in 1930 (NY). Calhoun Co.: Apalachicola, *Mohr & Sargent* in 1898 (US), *Parker* s.n. (NY); near Apalachicola, *Chapman herbarium 474a* (A, GH, NY); Chipola River, east of Clarksville, *Godfrey 56344* (FLA, GH). Escambia Co.: Escambia River near Pensacola, *Sheppard* in 1932 (NY). Franklin Co.: Apalachicola River, *Godfrey & Redfearn 55343* (FLA,

GH, NY); Crooked River, north of Carrabelle, *Godfrey 61749* (FLA). Holmes Co.: Between Chapley and Bonifay, *Godfrey 56366* (DUKE, FLA, GH, NY, UC, US); west of Millers Crossroads, *Godfrey 56403* (FLA, GH). Jackson Co.: West of Cottondale, *Godfrey 56362* (FLA, GH, UC). Leon Co.: West of Tallahassee, *Godfrey 58780* (FLA). Liberty Co.: 6 miles south of Telogia, *Godfrey 59373* (FLA, GH); southeast of Telogia, *Godfrey 61752* (FLA). Wakulla Co.: West of Crawfordville, *Godfrey 58229* (FLA, GH); north of Crawfordville, *Godfrey 59372* (FLA, GH, NY, UC); 30 miles southwest of Tallahassee, *Clewell & Hebb 586* (FLA). Walton Co.: Near Cluster Springs, *Godfrey & Harrison 55399* (FLA, GH, UC, NY); south of De Funiak Springs, *Godfrey 58256* (FLA, GH, NY), *Godfrey 59020* (FLA). GEORGIA. Pierce Co.: Without definite locality, *Godfrey 63251* (FLA). LOUISIANA. St. Martin Parish: St. Martinville, *Langlois* in 1886 (US). St. Tammany Parish: Slidell, *Lemaire 675* (FLA). Tangipahoa Parish: Hammond, *Wilson 346* (FLA); east of Hammond, *Innes & Warnock 722* (GH). Washington Parish: Northeast of Pine, *Correll 9231* (GH). MISSISSIPPI. Jackson Co.: Biloxi, *Tracy 6754* (GH, K); north of Escatawpa, *McDaniel 4055* (FLA). Pearl River Co.: West of Picayune, *Sargent 7943* (FLA). Stone Co.: East of Wiggins, *Kral 16520* (FLA). NORTH CAROLINA. Cumberland Co.: Fayetteville, perhaps cultivated, *Rankin* in 1930 (FLA).

Although the existence of an odorless *Gelsemium* was recognized early in the 19th century, *G. rankinii* was not fully described until 1928. In 1927, H. A. Rankin, a nurseryman in Hallsboro, North Carolina, sent the first of a series of collections of living material of *G. rankinii* to J. K. Small at the New York Botanical Garden. Rankin had noted, among other things, that this "Waccamaw river variety of *Gelsemium*" differed from *G. sempervirens* in its inodorous flowers, later flowering season, and preference for a wetter habitat. Small noted additional differences between these two species in the distribution of bracteoles on the pedicels, shape of the sepals, size and shape of the capsule, and seed characters. Small, in general, accurately characterized *G. rankinii* in his original description of this distinctive species, but perhaps because of the attenuated description and slightly inaccurate key (the leaf-base and anther characters he cites as distinguishing *G. rankinii* and *G. sempervirens* are unreliable) in his *Manual of the Southeastern Flora* (1933), few subsequent workers in the southeastern flora have recognized two species in the region. The majority of collections of *G. rankinii* in herbaria initially have been identified as *G. sempervirens*, but in the late 1950's R. K. Godfrey accurately distinguished between these two species in his herbarium annotations and extensive field collections. Later, Duncan and DeJong (1964) discussed the morphological, ecological, and phenological differences between the two. Because of its occurrence in very wet sites and the ease with which it is confused with the often sympatric *G. sempervirens*, it is probable that *G. rankinii* is more common in the field than might be indicated by its relatively low representation in herbaria.

3. **Gelsemium elegans** (Gardn. & Champ.) Benth. Jour. Linn. Soc. 1: 90. 1857.

Medicia elegans Gardn. & Champ., Hook. Jour. Bot. 1: 324. 1849. Holotype: K!

959 *Leptopteris sumatrana* Blume, Mus. Bot. Lugd. Bat. 1: 240. 1849.
960 *Gelsemium sumatranum* Boerl. Handl. 2: 448. 1899.

Vine to 3.5 m. tall; leaves elliptic to ovate, the blades 6–13 cm. long, sometimes cuspidate, evergreen, the petioles 0.5–1.2 cm. long; flowers numerous, inflorescence terminal or axillary; corolla 1.2–1.7 cm. long including the lobes 0.3–0.8 cm. long, bright- to orange-yellow, odorless (or rarely malodorous?); sepals lanceolate, acuminate, 3–4 mm. long; pedicels 0.3–1.0 cm. long, ebracteolate or with a single subtending bracteole; capsules ovate-elliptic in outline, 0.8–1.5 cm. long, inflated; seeds brownish, 3–4 mm. in diameter, including an inciso-dentate wing ca. 1–2 mm. wide; $n = 8$. Flowering September to December and occasionally at other times. In fruit March and April. FIG. 2a–f.

DISTRIBUTION. Sea level to 6000 feet. Climbing on shrubs and trees in scrub and open woodlands. Assam, northern Burma, northern Thailand, Laos, Viet Nam, southern and southeastern China, Sumatra, and northern Borneo. FIG. 3.

Specimens examined: **Borneo.** BRITISH NORTH BORNEO: From A. B. C. Francis, resident of the interior, *Gibbs 3130* (BM, US). **Burma.** Hkinlum, *Kingdon-Ward 21632* (A, BM); Kachin Hills, *Kingdon-Ward 9020* (A); Hookum Valley to Ava, *Hb. Griffith 3732* (K); Myitkina district, *Lace 6041* (K); Pangyang, Manglon State, *Dickason 9789* (A); Sumpra Bum, *Kingdon-Ward 20566* (A, BM); Wa States, *Maung Po Khant 15216* (K). **China.** FUKIEN: Foochow, *Warburg 5780* (A); Inghok, *Chung 3219* (UC). HAINAN: Dung Ka to Wen Fa Shi, *Chun & Tso 43755* (A, NY, UC); without definite locality, *Liang 64088* (K, NY), *Liang 64203* (NY), *Tang 450* (A), *Wang 35189* (NY, US), *Wang 36650* (A, NY). KWANGSI: Pin-lam, *Ko 55585* (A); Po Yam Shan, *Tsang 22925* (A); Shap Man Taai Shan, *Tsang 22029* (A, BM), *Tsang 24597* (A, NY); Tou Ngok Shan, *Tsang 23174* (A); Tung Loo, *Ching 5645* (A, UC, US); Tsin Hung Shan, *Ching 6860* (A, NY, UC, US); Yao Shan, *Wang 40048* (A); without definite locality, *Chen 91254* (A). KWANGTUNG: Au Tsai, *McClure 3534* (NY); Chung Tung, Tai Tsan, Ying Tak, *Tsang & Wong 3188* (UC); Kwai Shan, *Tsang 28553* (A); Lin Fa Shan, *Tsang 25748* (A); Lofan Mts., *Ford* s.n. (NY); Lofoushan, east river region, *Ho 60162* (NY); Lofoushan Mts., *Tsiang 1777* (A); Naam Kwan Shan, *Tsang 20260* (K, NY); Nam Shan, *Tsang 28874* (A); Ngong T'in Lo Shan, *Taam 347* (A); Shaan Sam village, *McClure 13291* (UC); Sha Lo Shan, *Taam 198* (A); Sinnei district, *T. Ying 2705* (K); Tung Koo Shan, *Tsang 21607* (K, NY, UC); Wan Tong Shan, Tai Tsan Ying Tak, *Tsang & Wong 2703* (UC); Wat Shui Shan, *Wang & Ling 7425* (UC); Weishang, Sunyi, *Tsiang 2705* (NY); Wong Chuk I and vicinity, *Lau 2173* (A); Wu Kan Tin, *Tsiang Ying 83* (A, UC); Wui Shui, *Tang & Fung 31* (NY); Yang Shan and vicinity, *Tsui 693* (K, NY, UC, US); Yun-fou, *Wang 354* (A, UC, US); Yung-Yun city and vicinity, *Lau 799* (A, NY), *Lau 915* (A, NY). YUNNAN: Fo Hai, *Wang 76247* (A), *Wang 77396* (A); Hsian-meng-young, *Wang 80994* (A); Keng-Ma, *Wang 72863* (A); Meng-soong, Dah-meng-lung, Che-li Hsien, *Wang 77992* (A); Mengtz, *Hancock 243* (K); Meng-tsze, *Henry 10452* (A, K, NY, US); Mar-li-po, Sze-tai-po, *Feng 13954* (A); Mar-li-po, Tung-ting, *Feng 13457* (A); Ping-pien Hsien, *Tsai 55136* (A), *Tsai 61880* (A); Si-chour-hsien. Faa-doou, *Feng 12118* (A); Si-chour-hsien, Shiang pyng-shan, *Feng 11485* (A); Tsing-pian, *Tsai 52403* (A); without definite locality,

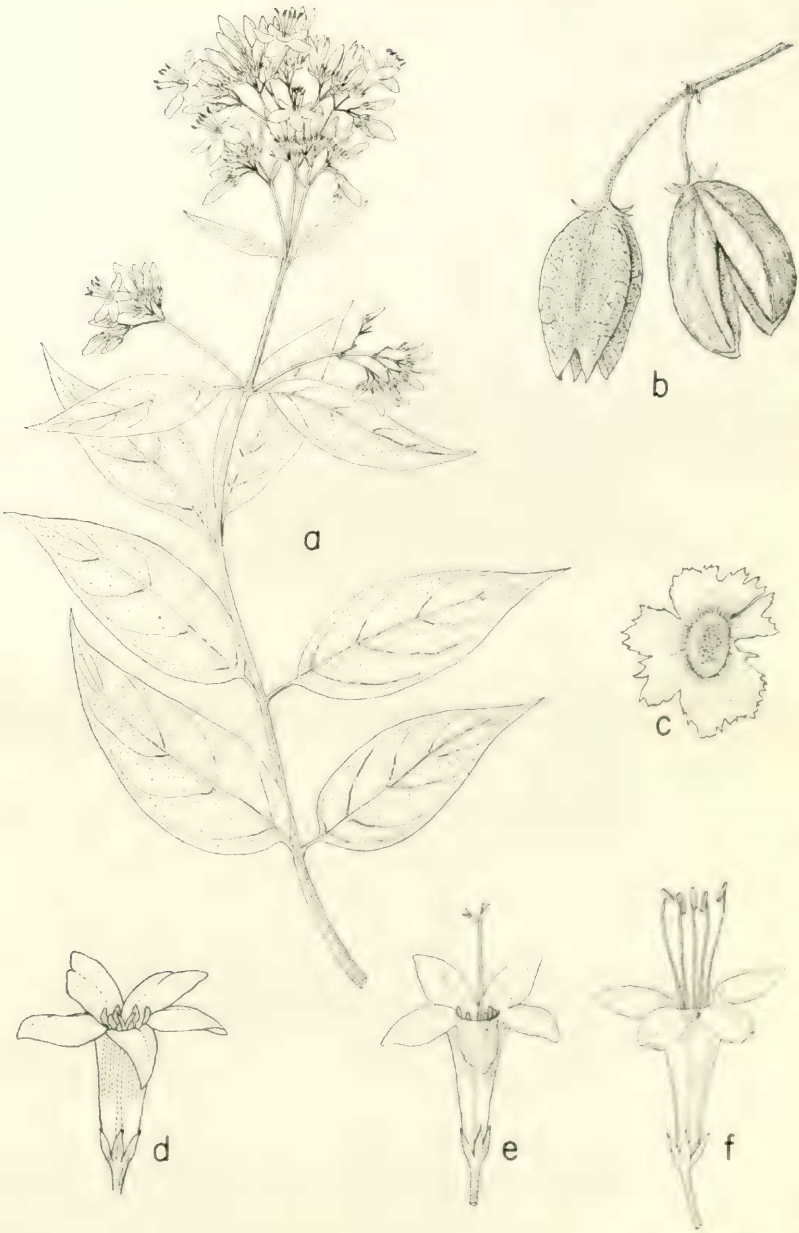

FIG. 2. Characters of *Gelsemium elegans*. a, portion of flowering stem, × 0.5; b, mature capsules, × 2; c, seed, × 5; d, short-homostyle flower, × 2; e, long-styled flower, × 2; f, short-styled flower, × 2.

Forrest 9214 (A). **Hong Kong.** *N. K. Chun 40251* (K); Kow-loon, *Lamont 467* (A); Lan-tao Island, *Lamont 467* (BM); Lo Fan Shan, *Anonymous* in 1883 (GH); New Territory, *Hb. Hongkong 1818* (A); without definite locality, *Wright 609* (GH, K, US). **India.** ASSAM: Jabocka (= Zoboka), Naga hill, *Prain's col-*

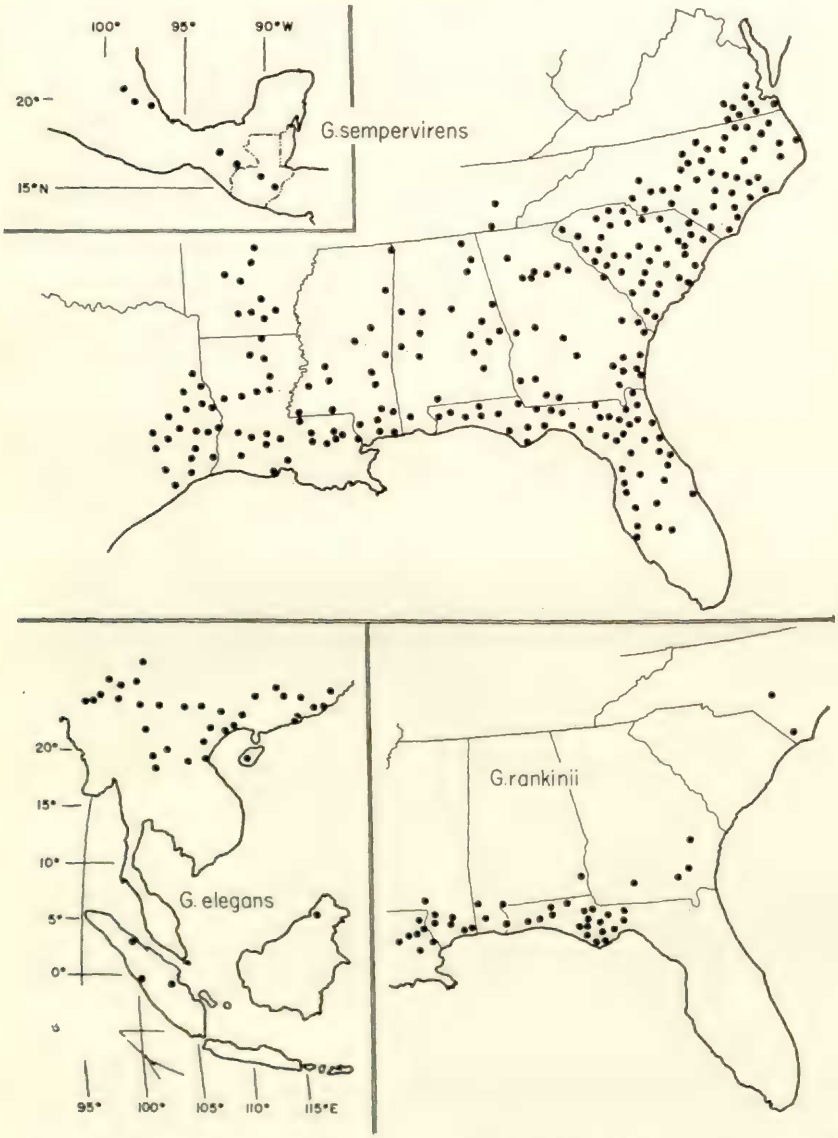

FIG. 3. Distribution of *Gelsemium* species. TOP, distribution of *G. sempervirens* in the southeastern United States and (INSET, upper left) Mexico and Guatemala. LOWER LEFT, distribution of *G. elegans* in southeastern Asia. LOWER RIGHT, distribution of *G. rankinii* in southeastern United States.

lector 959 (A); Lushai Hills, *Parry 322* (K). **Indonesia.** SUMATRA: Maranti, *Rahmat Si Boeea 6116* (A); Mt. Singalan, *Beccari 7* (K), *Beccari 355* (BM). **Laos.** Muang Huang, Wiengchan, *Kerr 20816* (K), *Kerr 200116* (BM). **Thailand.** Pu Huat (Nan), *Kerr 4996* (BM, K). **Viet Nam.** ANNAM: Thanhhoa, *Poilane 1893* (A). TONKIN: Hoa Binh, *Petelot 1906* (NY, US); Kau Nga Shan, *Tsang 30578* (A, K); Kun-Me-Tawng-Mê-Ping, *Garrett 1258* (K); Ouonbi, *Anonymous* in 1885 (A); Taai Wong Mo Shan, *Tsang 27326* (A, K), *Tsang 29611* (A, K).

BREEDING SYSTEM

Gelsemium sempervirens and *G. rankinii* are exclusively distylous, but *G. elegans* has both distylous and homostylous races. The distylous condition in the genus seems first to have been observed by Walter (1788), although it was overlooked by a number of subsequent workers (see Gray, 1873). Distyly in *Gelsemium* is characterized by the occurrence of two types of plants in populations of each species. Some individuals have long-styled flowers, short stamens, and small pollen; others, have short-styled flowers, long stamens, and larger pollen grains (TABLE 4). These two forms also differ in their compatibility relationships (TABLE 2).

TABLE 2. **Results of interspecific and intraspecific pollinations in Gelsemium**

CROSS	NUMBER OF FLOWERS USED	NUMBER OF SEEDS PRODUCED	PER CAPSULE AVERAGE NUMBER OF SEEDS
Interspecific pollinations:			
G. rankinii × *G. sempervirens*	25	5	0.2
G. sempervirens × *G. rankinii*	18	86	4.8
Intraspecific pollinations:			
G. SEMPERVIRENS:			
long selfed, or × long	99	73	0.7
short selfed, or × short	40	53	1.3
AVERAGE			0.9
long × short	58	765	13.2
short × long	28	307	11.2
AVERAGE			12.4
G. RANKINII			
long selfed, or × long	12	0	0.0
short selfed, or × short	25	56	2.2
AVERAGE			1.5
long × short	11	157	14.3
short × long	14	369	26.4
AVERAGE			21.0

The breeding system of *Gelsemium rankinii* and *G. sempervirens* was investigated by conducting a series of self-pollinations, pollinations among long-styled plants, and pollinations among short-styled plants (termed "illegitimate pollinations" by Darwin, 1877), as well as pollinations between long- and short-styled plants ("legitimate pollinations"). The results of the illegitimate pollinations (TABLE 2) indicate that a strong incompatibility system is present in both species since such pollinations result in a seed production that is much lower than seed production following legitimate pollinations. The long-styled form of both species seems to exhibit a stronger self-incompatibility than does the short-styled form. Legitimate pollinations produced a high seed set and it is assumed that in nature the reciprocal differences in position of stigmas and anthers of the two forms enhance legitimate pollinations by insects.

The breeding system of the distylous race of *G. elegans* is unknown, but since the morphological differences between the long- and short-styled forms of this species parallel those that exist in the American species, I assume it has an incompatibility system similar to that of its New World relatives. The homostylous race of *G. elegans* is a short-homostyle, i.e., the flowers have the style length of the short-styled form and the anther

TABLE 3. **Population samples of Gelsemium sempervirens showing representation of plants with long- and short-styled flowers**

COLLECTION NUMBER		LOCALITY	NUMBER OF PLANTS WITH LONG-STYLED FLOWERS	NUMBER OF PLANTS WITH SHORT-STYLED FLOWERS
Ornduff	*6376*	Hoke Co., N. Carolina	30	20
	6388	Duplin Co., N. Carolina	24	27
	6389	Duplin Co., N. Carolina	24	21
	6394	Bladen Co., N. Carolina	22	15
	6702	Orangeburg Co., S. Carolina	13	25
	6704	Bamberg Co., S. Carolina	55	56
	6705	Calhoun Co., S. Carolina	15	17
	6707	Richland Co., S. Carolina	61	44
	6708	Wake Co., N. Carolina	30	37
Breedlove	*9005*	Chiapas, Mexico	14	11
		TOTAL	288	273

position and pollen grain size of the long-styled form (FIG. 2d; TABLE 4). The only living plants of *G. elegans* that were available to me belonged to this homostylous race and were self-compatible, as would be expected from the position of the reproductive organs. This occurrence of a short-homostyle race in a normally distylous species is unusual. In the majority of heterostylous species in other plant families (such as Primulaceae, Rubiaceae, and Turneraceae) in which homostylous plants occur, the latter are generally long-homostyles.

Data concerning the pollination biology of *Gelsemium* are scant. Two collections of bees visiting *G. sempervirens* have been made. My collection was made in North Carolina and was identified by T. B. Mitchell. The most common visitors to the flowers were males and females of the large-bodied *Emphoropsis laboriosa* (Fabr.) (Anthophoridae). In addition, smaller-bodied bees belonging to the genera *Dialictus* and *Ceratina* were also collected. In Virginia, Hurd (pers. comm.) has noted *E. laboriosa* as well as the bumblebee *Bombus impatiens* Cresson (Apidae) visiting flowers of *G. sempervirens*. It is probable that the larger-bodied bees are the chief pollinators of *Gelsemium*, since the shape and size of the corolla tube as well as the relative position of anthers and stigmas require relatively large-bodied insects to effect pollen transfer.

Population samples of *G. sempervirens* indicate that long- and short-styled plants are present in a 1:1 ratio (TABLE 3). This is probably also the case for *G. rankinii* (Duncan & DeJong, 1964).

Elsewhere in the Loganiaceae, heterostyly has been reported for *Mostuea* (Leeuwenberg, 1961) and has also been suggested for *Buddleia* (Leenhouts, 1962), although the latter genus requires further study. Otherwise, heterostyly is unknown in this family, although it occurs in the related Oleaceae and Rubiaceae. Despite the rarity of heterostyly in the Loganiaceae and its possibly independent evolutionary origin in this family, the morphological expression of heterostyly in *Gelsemium* is remarkably similar to that which exists in other unrelated distylous genera (Darwin, 1877; Vuilleumier, 1967).

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TABLE 4. **Measurements of style length, stamen length, and pollen size of heterostylous and homostylous Gelsemium flowers**

SPECIES	STYLE LENGTH	SAMPLE SIZE	STYLE LENGTH (with range in cm.)	STAMEN LENGTH (with range in cm.)	POLLEN SIZE (with range in μ; sample size)
G. sempervirens	Long	36	1.8 (1.2–2.3)	0.8 (0.7–0.9)	33.9 (31.5–36.4; 260)
	Short	38	0.8 (0.5–1.3)	1.6 (1.5–2.3)	37.0 (32.8–40.1; 200)
G. rankinii	Long	10	2.2 (1.8–2.4)	0.7 (0.6–0.9)	31.5 (28.1–34.2; 200)
	Short	10	0.7 (0.6–0.8)	1.8 (1.7–2.0)	36.1 (34.2–38.1; 200)
G. elegans	Long	10	1.2 (1.0–1.4)	0.5 (0.4–0.6)	27.7 (22.8–33.2; 180)
	Short	10	0.7 (0.5–0.8)	1.1 (1.0–1.4)	30.8 (25.6–38.0; 180)
	Homostyle	7	0.7 (0.6–0.8)	0.6 (0.5–0.7)	26.7 (24.0–30.8; 60)

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Department of Botany
University of California
Berkeley, California 94720